Aspects of the Reproductive Biology of Murray Cod, *Maccullochella peelii peelii*

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Aspects of reproduction in Murray cod, *Maccullochella peelii peelii*, in NSW tributaries of the Murray-Darling river system were studied. Murray cod has a distinct seasonal cycle; monthly gonadosomatic indices (GSI) and mean oocyte diameters were low between December and March, increased rapidly from June, presumably due to vitellogenesis, and were highest in October. Oocytes underwent group-synchronous development, but only one batch of yolky oocytes was spawned during the 4–5 week breeding season. Absolute fecundity ranged from 6,800 (total length, TL 480mm, weight 2.1kg) to 86,600 (1050mm, 22.7kg) eggs, and relative fecundity ranged from 3.2 to 7.6 eggs/g. Spawning was induced by a rise in water temperature to or above 20°C in spring. The presence of many consecutive year classes suggests that Murray cod spawn annually; however, between 1977 and 1980 relatively strong year classes were formed only in rivers that were at, or near flood levels during the breeding season.

No females and a few males had matured by 3 years of age. At 4 years of age, 77% of females (> 480mm, 2.1kg) and 72% of males (> 530mm, 2.3kg) were mature. All females and most males were mature at 5 years. In rivers, all cod larger than 590mm and 3.9kg were mature, but the smallest sexually-mature cod sampled from the impoundment, Lake Mulwala, was 610mm and 5.0kg. Management restrictions on the recreational and commercial fisheries for Murray cod, based on the results of this and previous studies are outlined.

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KEYWORDS: Australian inland fisheries, breeding season, fecundity, *Maccullochella*, maturation age, Murray cod, reproductive cycle.

INTRODUCTION

Despite the importance of the Murray cod, *Maccullochella peelii peelii* (Mitchell) in the inland fisheries of south-eastern Australia, and the decline in abundance and reduction in distribution since the 1950's (Rowland 1989), no quantitative study of the reproductive biology of the species in the Murray-Darling river system has been published. Gooley et al. (1995) studied the reproductive cycle and gonadal development of Murray cod in Lake Charlegrark and adjacent farm dams in western Victoria; however, this is an introduced, self-maintaining population and aspects of its biology differ from natural populations (Anderson et al. 1992; Gooley 1992).

Studies of Murray cod held in earthen ponds have provided some information on the reproductive biology of the species. Cod spawn adhesive eggs onto firm substrates such as hollow logs, pipes and clay banks in spring and early summer (Lake 1967a; Rowland 1983; Cadwallader and Gooley 1985). Lake (1967a) found that a slight 'runoff' of water into a pond induced cod to spawn, but later studies by Rowland (1983) and Cadwallader and Gooley (1985) demonstrated that spawning was not dependent on a rise in water level in ponds. Emryology and larval development in Murray cod were described by Dakin and Kesteven (1938) and Lake (1967b), and there is paternal protection of eggs during incubation (Rowland 1983). The diet and factors affecting the survival of Murray cod larvae in earthen ponds were determined by Rowland (1992). Artificial breeding techniques, including the hormone induction of ovulation and spawning have been developed (Cadwallader and Gooley 1985; Rowland 1988).

Rowland (1985) conducted research into aspects of the biology of Murray cod to provide a basis for management of the species in NSW. The reproduction component of that study is reported in this paper. Objectives were to describe the reproductive cycle and fecundity of Murray cod from tributaries of the Murray-Darling river system, and to determine the effects of water temperature and water levels on spawning, the timing and length of the breeding season, and the age and size at maturity of males and females from different populations.

MATERIALS AND METHODS

Murray cod were sampled (1978–1984) from five sites in the Murray-Darling river system (see Fig. 1 in Rowland 1998), with the exception of the Darling River, using techniques described by Rowland (1985). Some fish were sampled from the catches of professional and recreational fishers. Cod were sampled irregularly from the Murray and Murrumbidgee rivers and the impoundment, Lake Mulwala in southern NSW, and Gwydir River in the northern part of the Murray-Darling river system (Fig 1 in Rowland 1998) to determine age and size at maturity, and fecundity. In addition, data were collected from Murray cod sampled monthly from the Edward and Wakool rivers over an 11-month period between May 1983 and March 1984 to describe the gonadal cycle and to determine the breeding season. During September, October and November sampling was confined to a 10km section of the Wakool River to more closely evaluate the effects of water temperature and changes in water level on brood-fish and the breeding season.

Gonadal cycle and fecundity

Each fish was measured (TL to the nearest mm) and weighed (to nearest 10g). The gonads were removed, assigned to a stage of the Gonadal Maturity Scale (Table 1) and placed in Bodians fixative. In the laboratory, all fatty tissue and excess fluid were removed from each gonad before weighing to the nearest 0.1g. The gonadosomatic index (GSI) was calculated as the percentage of gonad weight of the total body weight; the mean monthly GSI for each sex was determined.

The tunica was removed from both ovaries of each female and all oocytes larger than approximately 0.2mm diameter were separated manually from the ovarian tissue. This was aided by vigorous shaking in Bodians fixative. No attempt was made to free the oogonia, perinuclear and other early stage oocytes. A random subsample of 100 oocytes was removed after inverting the container several times to ensure even distribution of oocytes. The diameter of each oocyte in the subsample was measured using an eye-piece micrometer. The oocytes were assigned to three size-classes based on diameter; 0.2–1.0mm; 1.1–2.0mm; >2.0mm. The total number of oocytes in each size-class in 5 adult females was expressed as a percentage frequency for each month, and a mean monthly diameter of the largest size-class was also determined.

Ovaries of mature (stage IV, Table 1) females captured in September and October were used to estimate fecundity. The ovaries were prepared as described above. All freed oocytes, and then three 3g subsamples from each female were weighed; oocytes greater than 2mm diameter in each subsample were counted. The mean number of presumably yolky oocytes (> 2mm) in the three subsamples was determined and used to estimate the fecundity of each female by direct proportion.

TABLE 1

Gonad maturity scale describing the appearance of the gonads, abdomen and vent of Murray cod.

Stage	Female	Male
I immature A	Ovaries thin, slightly rounded; pale pink, translucent; (1 and 2 year old).	Testes thin, strap-like; pale, translucent.
B	Ovaries rounded, cylindrical; pale pink, translucent; up to 80mm long, 10mm wide; sometimes white oocytes (to 1mm) visible in clear fluid; (3 and some 4 year old).	Testes thickening; opaque.
II developing virgin or recovering spent	Ovaries rounded; pale pink; oocytes (to 1mm) visible to naked eye, throughout most of ovary.	Testes flattened; pale creamy/pink.
III developing	Ovaries enlarging, rounded; occupy to ¼ body cavity; oocytes 1–2mm. Abdomen slightly rounded; vent pale pink.	Testes enlarging; creamy/pink.
IV mature	Ovaries occupy to ½ body cavity; pale/amber oocytes 2–3mm; also small (1mm) white oocytes visible. Abdomen distended; vent swollen, pink/red.	Testes enlarged, rounded on edges; white/creamy; small blood vessels on surface. Abdomen not distended; vent pale.
V running-ripe	Translucent oocytes (3mm) run freely from oviduct with pressure; ovaries pinkish/pale red, occupy > ½ body cavity. Abdomen very distended; vent swollen, red/purple.	Testes full, rounded; white; milt with firm abdominal pressure. Abdomen not distended; vent pale/pinkish, slightly swollen.
VI spent A	Partially; ovaries rounded; occupy ½ cavity, but smaller than IV and V; many large (3mm) translucent oocytes; some parts of ovaries clear; some small (1mm) white oocytes visible.	
B	Completely; ovaries rounded; occupy < ¼ cavity; red/dark pink; wall loose in recently spent females; few oocytes visible. Abdomen not distended, flabby.	Small amount or no milt on pressure; testes relatively small; creamy/pale pink; mottled appearance; walls loose; many distinct small blood vessels on surface.
VII resorbed	Ovaries < ½ cavity; walls loose; large blood vessels on surface; misshapen oocytes (2–3mm); clear and reddish patches throughout ovaries.	

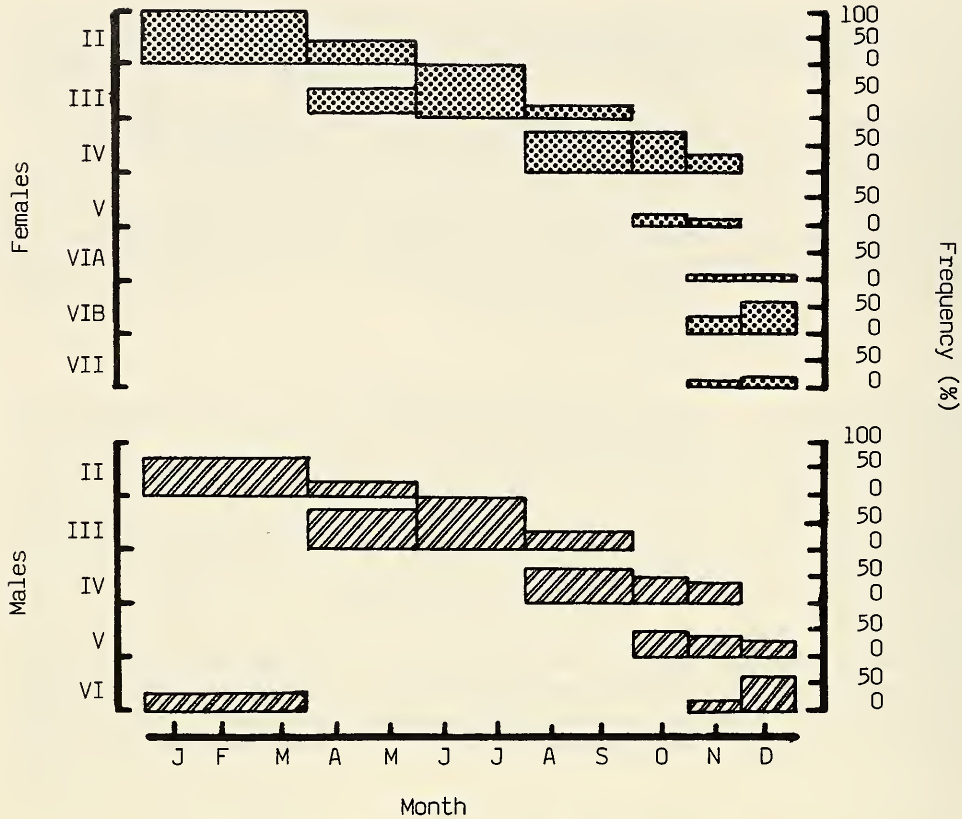

Figure 1. Seasonal changes in the relative frequency of gonadal maturity stages in Murray cod (of both sexes) from the Edward and Wakool rivers. The stages (I–VII) are described in Table 1.

Breeding season

To obtain data on the behaviour of broodfish, the duration of the breeding season and the factors inducing spawning in the wild, Murray cod were sampled using 20 gill nets (mesh sizes 10.2 - 25.4cm) and 5 drum nets (mesh size 12.7cm) from a 10 km section of the Wakool River between September and December. Water temperatures were recorded using a maximum-minimum thermometer placed permanently at a depth of 1.5m; changes in water level were recorded.

Age and size at maturity

Murray cod sampled from the Edward, Wakool, Murray and Gwydir rivers between September and December 1983, were used to determine the age and size at sexual maturity. Cod with gonads at stages IV to VII (Table 1) during this period were presumed to be mature. Otoliths and opercular bones were used to age the cod (Rowland 1985, 1998). After ageing, all fish were assigned to a year-class and the percentage frequency of year-classes from 1977 to 1980 was determined. To reduce the bias of mesh selectivity against smaller cod from the 1980 year-class, only cod captured between September and March were included in this analysis.

RESULTS

Gonadal cycle

There was a linear relationship between GSI and the percentage frequency of oocytes larger than 2mm diameter ($Y = 0.56X - 14$; $r^2 = 0.92$), indicating that GSI accurately reflects the gonadal state in Murray cod.

Most cod sampled between April and September contained gonads at stages III (developing) or IV (mature) (Fig. 1). The rapid increase in the proportion of oocytes greater than 2mm diameter, between June and October (Fig. 2) is presumably due to vitellogenesis. Mean oocyte diameters, the proportion of large, yolky oocytes, and GSI values were highest in October (Figs 2 and 3). "Running-ripe" (stage V) females and males were captured in October and November. Spent and partially spent cod were captured in November. The ovaries of fully spent females (stage VI B) contained very few residual, yolky eggs, and although an estimated 30 - 50% of oocytes remained in ovaries of partially spent females (stage VI A), most were large (3mm), spherical, translucent and ovulated, suggesting that the females were captured during spawning. By December, all females were spent or contained ovaries in which resorption had commenced. Between January and March all cod had spent or recovering gonads (stage II) and low GSI values.

Fecundity

The number of large (>2mm), yolky oocytes per female ranged from 6,800 (480mm, 2.1kg) to 86,600 (1050mm, 22.7kg). Absolute fecundity generally increased with increasing length and weight of females; however, there were large variations in the fecundity of similar-sized females (Fig. 4).

The relationship between fecundity and length is linear and represented by the equation:

$$Y = 115.17X - 48.9 \ (r^2 = 0.90)$$

where Y = fecundity ($x10^3$) and X = length in mm.

The relationship between fecundity and weight is quadratic and is represented by the equation:

$$Y = -389 + 5344X - 69.5X^2 \ (r^2 = 0.93)$$

where Y = fecundity and X = weight in kg.

The relative fecundity ranged from 3.2 to 7.6 eggs/g. The mean relative fecundity of different size-classes are shown in Fig. 5. Although only four fish were used to estimate fecundity of females over 11kg, the data suggest that relative fecundity decreases with increasing size and age in Murray cod.

Breeding season

During the period 24 September to 18 October 1983, water temperatures in the Wakool River ranged from 16 to 19°C, and pairs of mature cod (stages III or IV) consisting mainly of similar-sized males and females, were often captured in one drum net or within several meshes of each other in gill nets. The daily maximum water temperatures and the details of the reproductive condition of Murray cod captured from the Wakool River between 18 October and 5 November are shown in Fig. 6. Within 10 days of the water temperature reaching 20°C, two spent females, one "running-ripe" female, two "running-ripe" males and four mature (stage IV) females were captured. Although spent females were captured in late October and early November the first spent male was not captured until 24

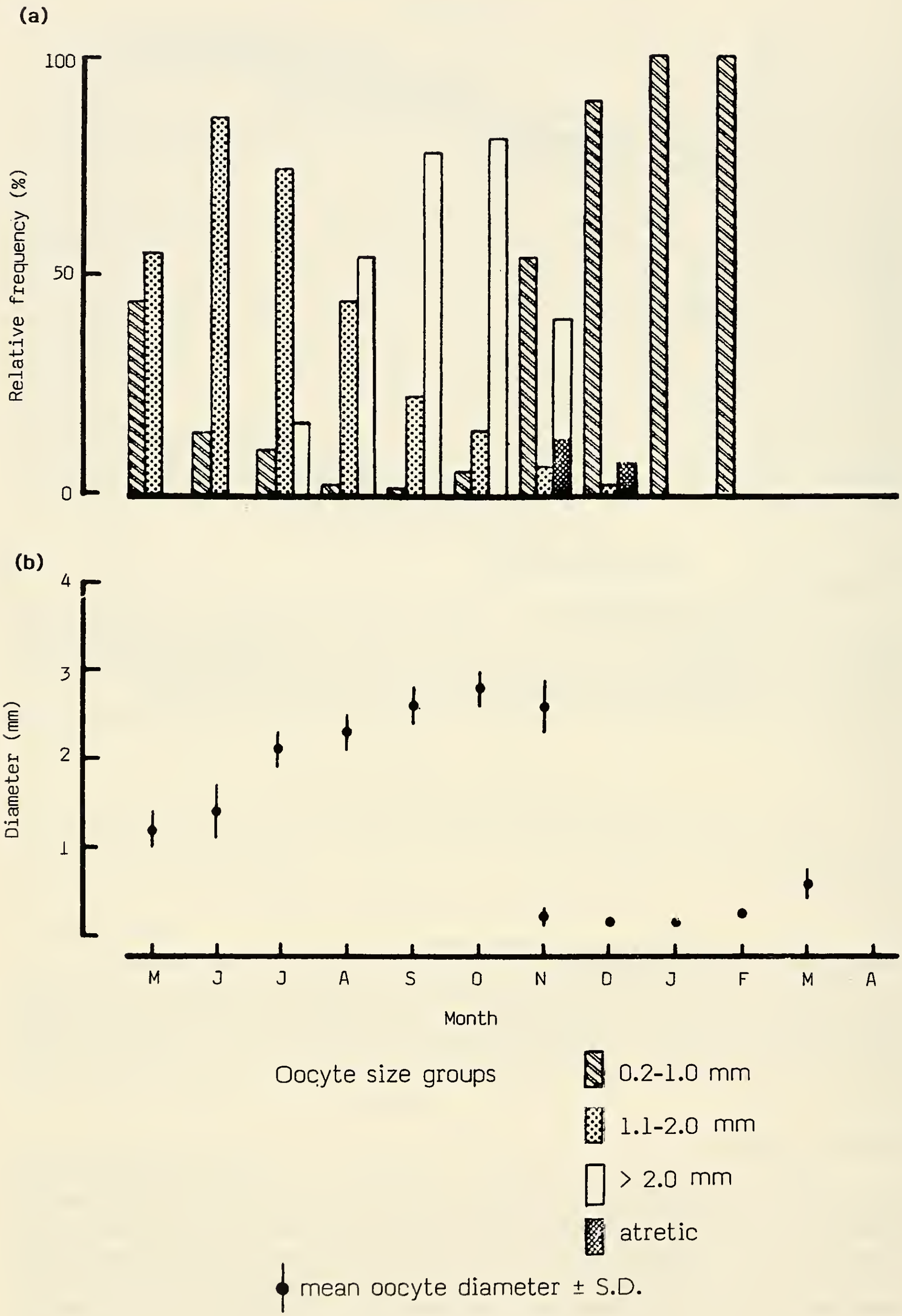

Figure 2. The occurrence of oocyte size groups during the period May 1983–March 1984, in Murray cod females from the Edward and Wakool rivers: (a) relative frequency; (b) mean monthly diameter.

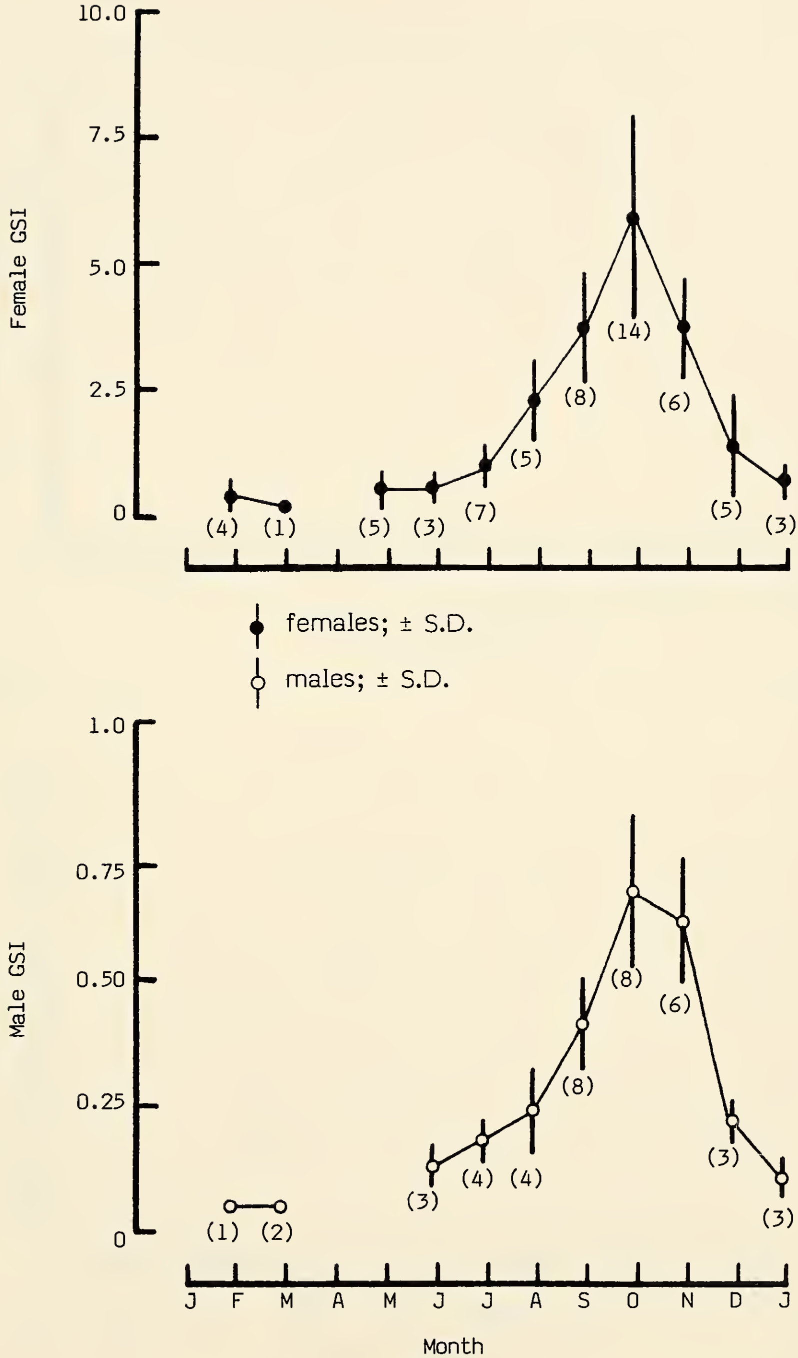

Figure 3. Mean monthly gonadosomatic indices (GSI) for the period May 1983–March 1984 in Murray cod from the Edward and Wakool rivers: (a) females; (b) males. Sample sizes in parentheses.

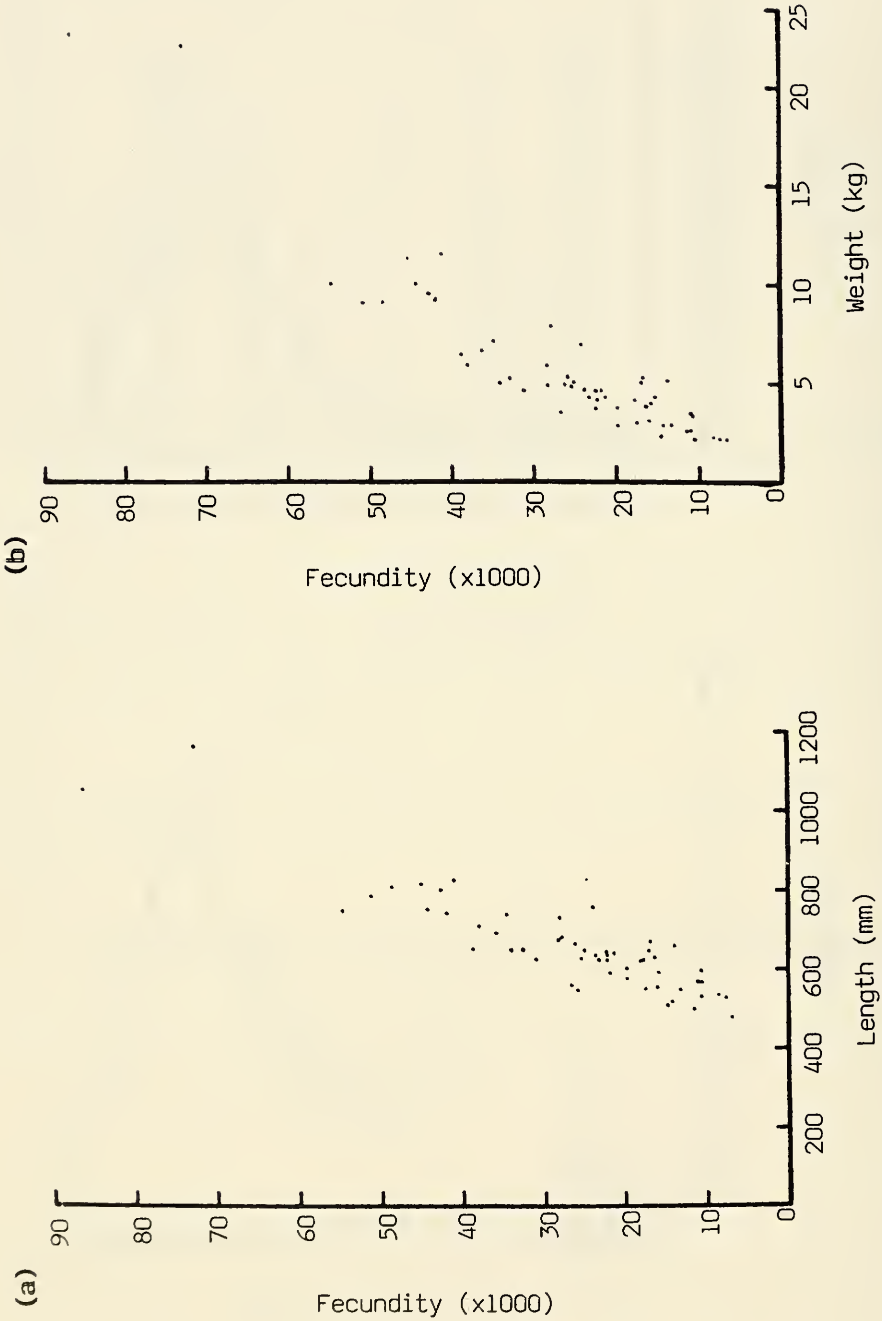

Figure 4. Relationship between fecundity and size of Murray cod females from the Murray, Edward, Wakool and Gwydir rivers: (a) related to length; (b) related to weight.

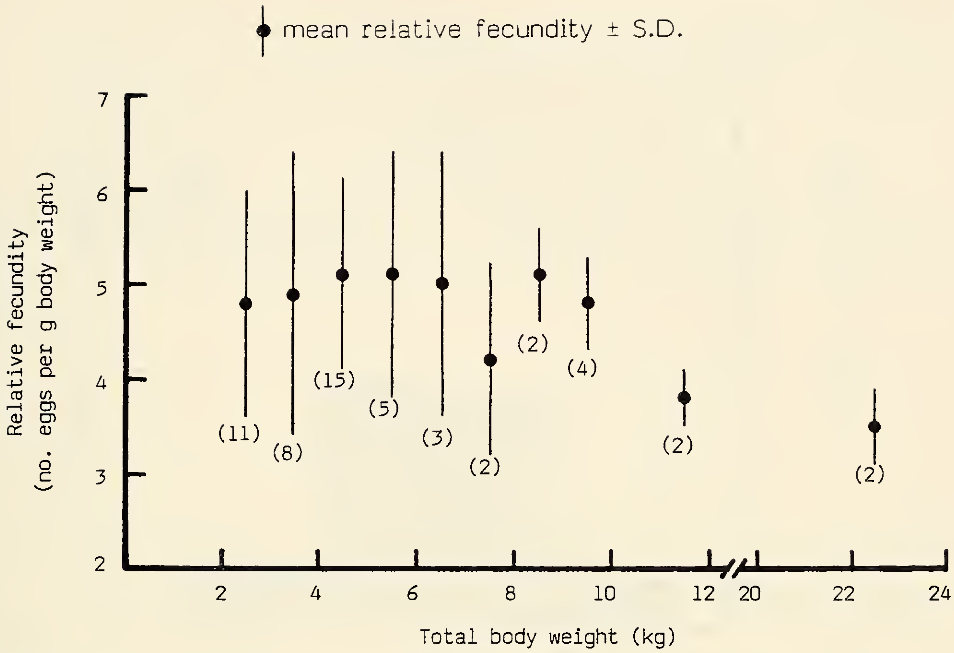

Figure 5. Relative fecundities in different size-classes of Murray cod females. Sample sizes in parentheses.

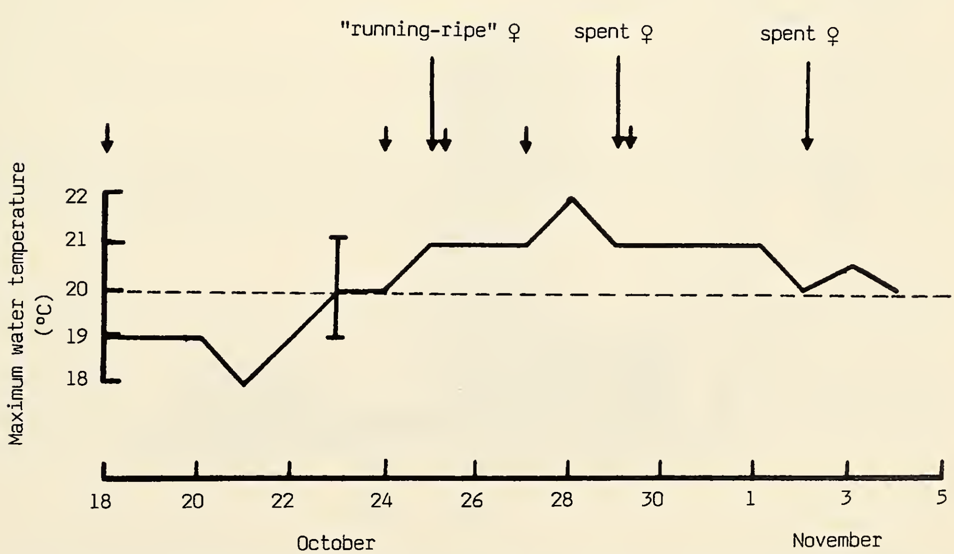

Figure 6. Water temperature and details of gonadal condition of Murray cod females captured from the Wakool River between 18 October and 5 November.

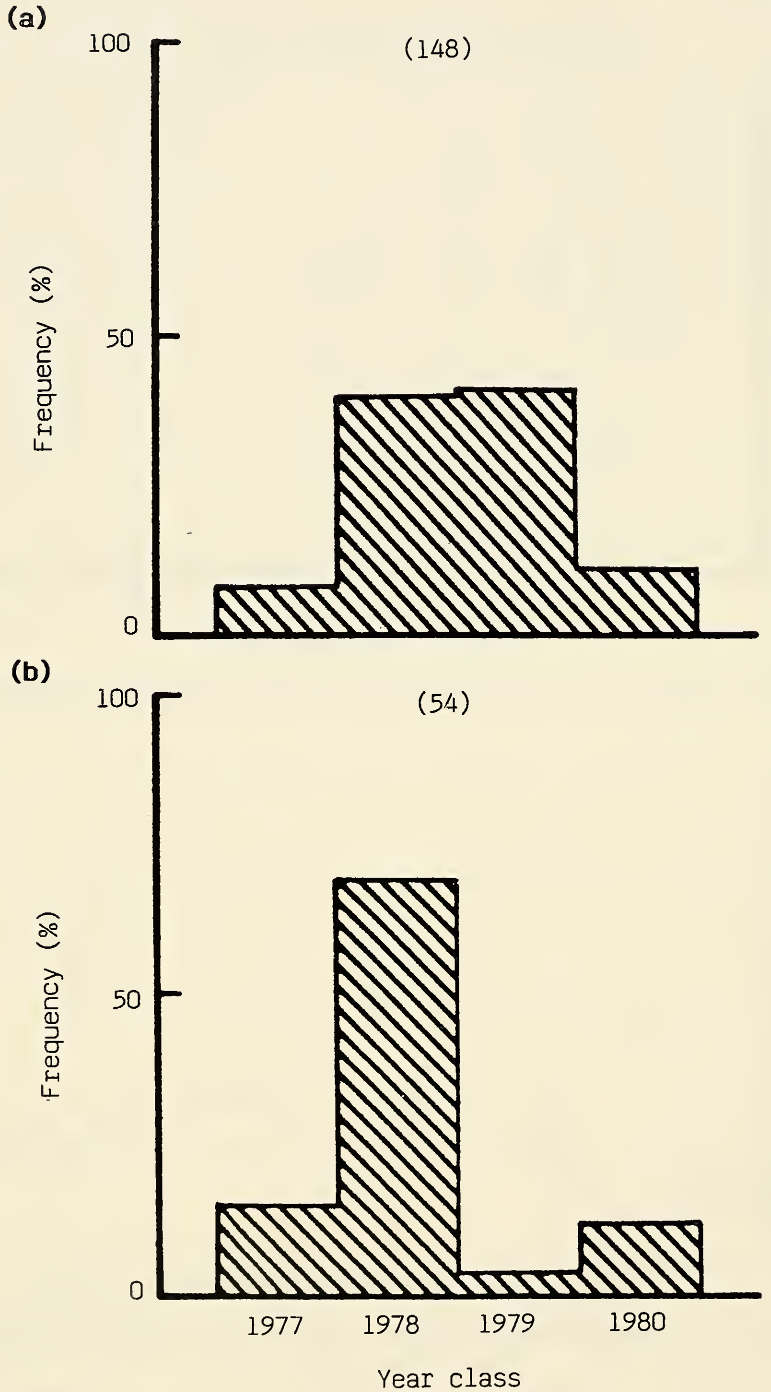

Figure 7. Recorded frequencies for four year-classes (1977–1980) of Murray cod: (a) from the Murray, Edward and Wakool rivers; (b) from the Murrumbidgee River. Sample sizes in paretheses.

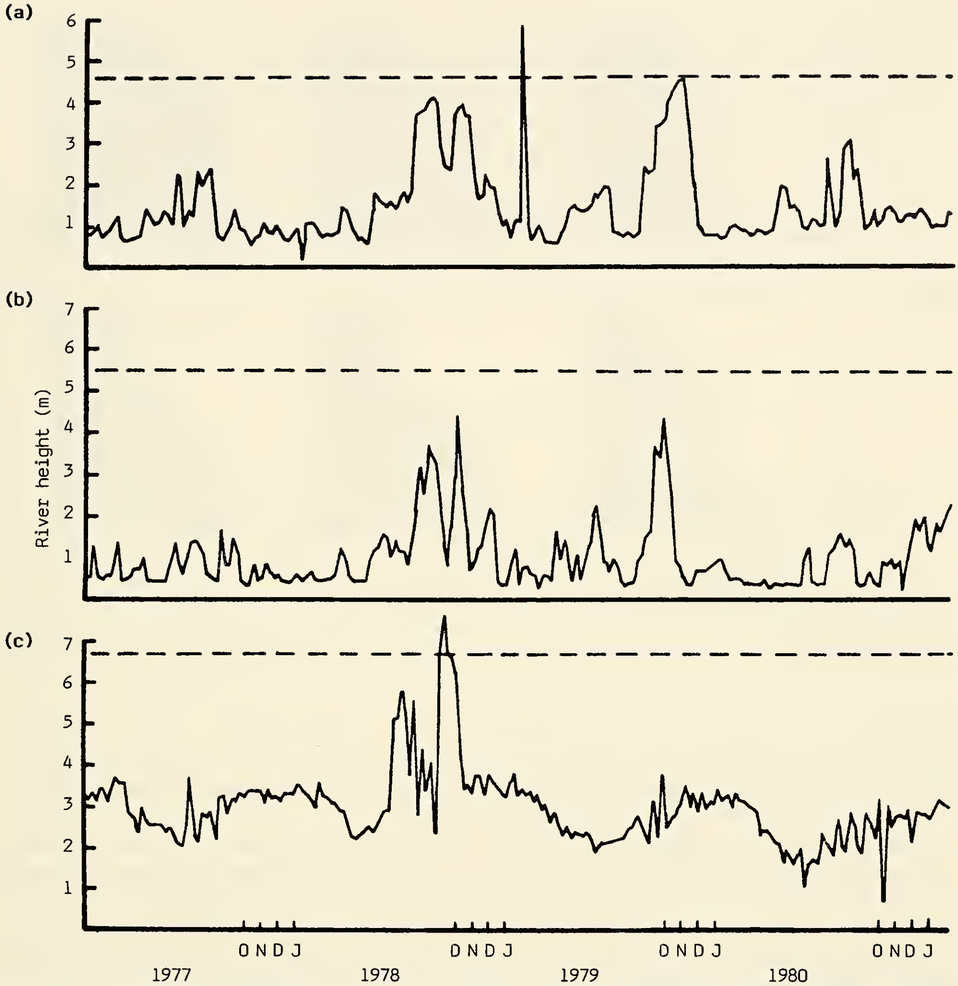

Figure 8. River heights related to flood levels (– – –) for the period January 1977 to January 1981: (a) in the Murray River (at the junction with the Wakool River); (b) in the Edward River (downstream of Stevens Weir); and (c) in the Murrumbidgee River (at Narrandera).

November. The data suggest that the actual spawning season lasted 4 to 5 weeks. Between 24 September and 24 November the water level decreased gradually by 60cm.

Mature and spent females, and "running-ripe" males were sampled from the Gwydir River between 1 and 5 October when water temperatures were 20 to 22°C. The water level in the river had been constant for approximately two weeks (Phil Forster, Bingara, personal communication).

Year-class frequencies

Murray cod representing each year-class between 1970 and 1980 were sampled from the Murray, Edward and Wakool rivers, and cod from 16 of the 17 year-classes between 1964 and 1980 were sampled from the Murrumbidgee River. The Murray cod (n = 25)

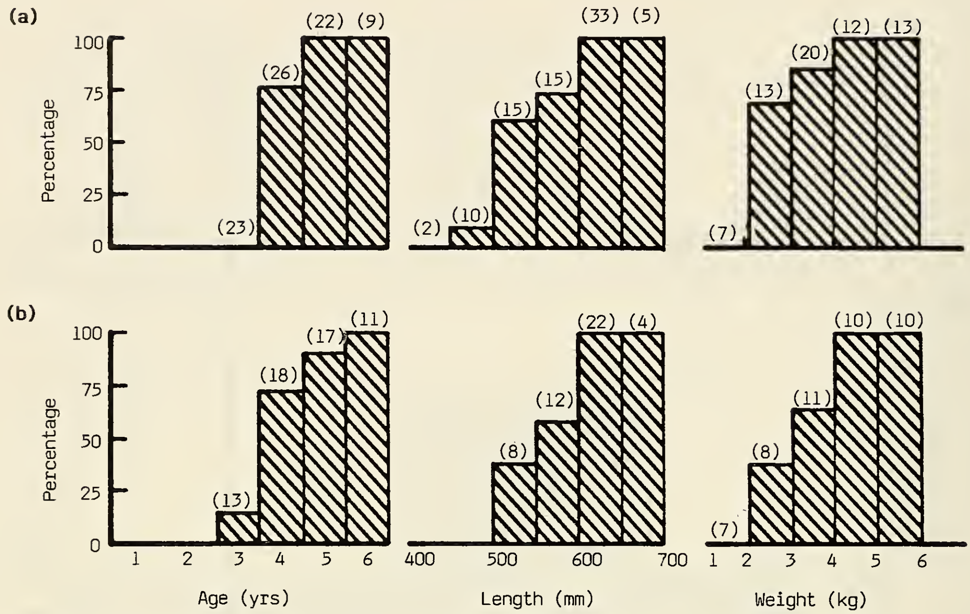

Figure 9. Percentage of mature Murray cod in each age, length and weight class: (a) females; (b) males. Sample sizes in parentheses.

sampled from the Gwydir River in October represented five year classes; 1976, 1978, 1979, 1980 and 1981. The presence of many consecutive year-classes in each river suggests that cod have spawned annually in these rivers.

The percentage frequencies of the 1977 to 1980 year-classes in the Murray, Edward, Wakool and Murrumbidgee rivers shows the 1978 year-class was strong in each river (Fig. 7). In 1978, all rivers were at or near flood level during October and November (Fig. 8). Consequently the breeding season probably coincided with flood conditions and the strong 1978 year-class is evidence for high survival of larvae under these conditions. This is supported by the presence of a relatively strong 1979 year-class in the Murray, Edward and Wakool rivers, but a poor year-class in the Murrumbidgee River (Fig. 7). In October and November 1979, the former three rivers were near flood level but the Murrumbidgee River did not rise above 3.8m at Narrandera (Fig.8). In 1977 and 1980, all rivers remained at low levels during spring and summer, and these year-classes were poorly represented in these southern tributaries.

Age and size at maturity

The percentages of mature Murray cod in each age and size-class are shown in Fig. 9. All 1 to 3 year old females were immature. One and 2 year old cod contained thin, rounded, translucent ovaries (stage 1A) while those of 3 year old females were cylindrical and sometimes contained oocytes (to 1mm diameter) that were visible to the naked eye in clear ovarian fluid (stage 1B) (see Table 1). Seventy seven percent of 4 year old females were mature. Immature cod of this age had ovaries with numerous, white oocytes less than 2mm in diameter (stage 1B). All 5 and 6 year old females were mature. The smallest mature female sampled in this study was 480mm and 2.1kg; all females 590mm and 3.9kg or larger were mature.

All 1 and 2 year old males were immature. Fifteen percent of 3 year old cod were "running-ripe" in October and were presumed to be mature. However, the viability of the sperm from these fish was not determined and it is possible that it was non-viable and/or that these males were precocious. The smallest of these cod was 530mm and 2.3kg. Seventy two percent of 4 year old, most 5 year old and all 6 year old males were mature. All males of 585mm and 3.4kg and larger were mature.

Seven of the nine 4 year old females (77%) sampled from Lake Mulwala were mature and the smallest of these was 610mm and 5.0kg. The 2 immature females were 630mm and 5.8kg, and 640mm and 5.5kg. No 5 year old females were sampled from the lake, but all 6 and 7 year old females (n=7) were mature. Eighty percent of 4 year old males were mature; the smallest was 625mm and 5.4kg. No older males and no 3 year old cod were sampled from Lake Mulwala.

DISCUSSION

Reproductive cycle and the breeding season

The Murray cod, like many other temperate fishes, has a distinct annual reproductive cycle. Increasing GSI and mean oocyte diameters from June onwards suggest that gonadal recrudesence is initiated by increasing temperature and/or photoperiod as in many other teleosts (see Lam 1983). Murray cod exhibits group-synchronous oocyte development (de Vlaming 1983), with two or three distinct batches of oocytes distinguishable in the ovary in most months (Fig. 2a). The batch of smallest oocytes (< 1.0mm) would consist of oogonia, perinuclear and other primary oocytes for the following breeding seasons. Although two batches of larger oocytes (1.0–2.0mm; >2.0mm) are present in the prespawning ovary, previous studies by Rowland (1983, 1988) suggest that only one batch completes vitellogenesis to become the numerous, large (3.0mm), yolky oocytes that are spawned and fertilised. The fate of the intermediate batch, which presumably have not completed vitellogenesis, is not known; they may be spawned days or weeks later, or resorbed along with other ovarian material during post-spawning gonadal regression as has been reported in other species (Foucher and Beamish 1980; Mayer et al. 1990).

The reproductive cycle of Murray cod culminates in a relatively short, well-defined breeding season. Spawning is temperature-dependent and so the actual season is expected to vary latitudinally. In the current study, spawning in the southern Wakool River commenced after water temperatures rose above 20°C in late October, whereas in the northern Gwydir River spent females were caught in early October when temperatures were between 20 and 22°C. Rowland (1983) found that in four consecutive breeding seasons at the Inland Fisheries Research Station, Narrandera, most Murray cod spawned in earthen ponds when the temperature rose to or above 20°C, and cod held in ponds at hatcheries in northern NSW spawn regularly each year when water temperatures reach 20°C in late September and early October (Ray Mepham, Elsmore and Phil Forster, Bingara, personal communication). In ponds at Lake Charlegrark, near the southern limit of its natural range, most spawnings occurred during November at temperatures between 16.5 and 23.5°C (Cadwallader and Gooley 1985; Gooley et al. 1995). Conspecific populations of fishes are known to exhibit local differences in their reproductive life histories (Leggett and Carascadden 1978; Bye 1984; Mann et al. 1984) and the cooler temperature regime at this southern locality may cause the different response to the rising temperatures during spring. Other factors such as the role of photoperiod, the demography of cod in ponds and varying methods of actually measuring water temperature may also account for the variation in spawning temperatures reported.

Individual females probably spawn all or most of the largest batch of oocytes in one short period. Ovulated oocytes in the small number of "running-ripe" and partially spent females that were caught during this study (Fig. 1) were large and translucent, indicating that spawning was either occurring or imminent. Rowland (1983) found that only one of 36 females was "running-ripe" when removed from eight ponds over four consecutive breeding seasons. These observations suggest that there is only a relatively short period between ovulation and spawning.

The relatively high catch rate of cod, including pairs, in September was probably a result of increased activity of broodfish associated with spawning site selection and mating. The difficulty in catching spent males in late October and November suggests that they are not involved in normal foraging behaviour and could be protecting the eggs and possibly larvae at the spawning sites.

All Murray cod sampled in December were either spent or contained ovaries with a large number of atretic oocytes, indicating that the spawning season was complete and that in some years at least, not all females spawn. As in some other species (Lam 1983) relatively high water temperatures and long photoperiod may induce normal gonadal regression in Murray cod. The data suggest that the spawning season lasted 4 to 5 weeks.

After Lake (1967a) reported that a slight "runoff" of water into a pond was necessary to induce Murray cod to spawn, subsequent literature (e.g. Roughley 1968; Llewellyn and MacDonald 1980; Pollard et al. 1980) stated that a rising river level or flood is required for Murray cod to spawn. Further research has shown that rising water levels are not required to induce spawning in ponds (Rowland 1983; Cadwallader and Gooley 1985) or in the wild (current study). The presence of many consecutive year classes in each of the Murray, Murrumbidgee, Edward, Wakool and Gwydir rivers suggest that Murray cod spawn annually in the wild irrespective of changes in water level. However, strong year-classes are only established when the breeding season coincides with high river levels or floods (Figs 7 and 8). These data support the hypothesis that the reduced frequency, extent and duration of flooding in the Murray-Darling river system caused by the construction of dams, high level weirs and levee banks has adversely affected larval recruitment, resulting in the dramatic decline of Murray cod since the 1950's (Rowland 1983, 1985, 1989, 1992).

Fecundity

The relative fecundity of Murray cod (3.2–7.6 eggs/g) is similar to the congeneric trout cod, *M. macquariensis*, (0.6–5.9 eggs/g) (Ingram and Rimmer 1992), but low compared to some other freshwater fishes, e.g. carp, *Cyprinus carpio*, (24–198 eggs/g) and perch, *Perca fluviatilis*, (91–473 eggs/g) (Gromov 1979; Volodin 1979). Absolute fecundity (6,800–86,600) is low compared to the smaller Australian percichthyids of the genus *Macquaria*, ranging from the Macquarie perch (*M. australasica*) which spawns 50,000 to 107,700 eggs to Australian bass (*M. novemaculeata*) and golden perch (*M. ambigua*) both of which may spawn over 500,000 eggs (Merrick and Schmida 1984). The large variation in the fecundity of similar-sized Murray cod (Fig. 4) is characteristic of many species; the fecundity of different stocks of the same species can also vary markedly (Bagenal 1978). The inclusion of cod from different rivers may have contributed to this variation. There was a linear relationship between fecundity and length in Murray cod, whereas in many species this relationship is exponential (Bagenal 1978). It is possible that the small sample size of cod over 10kg obscured an exponential relationship, particularly as it appears that relative fecundity decreases with increasing size and age in Murray cod (Fig. 5).

Age and size at maturity

Age or size at maturity in fishes is influenced by various demographic and environmental factors including growth rate (Stearns and Crandall 1984). Although Murray cod grow at different rates in rivers and impoundments in NSW (Rowland 1998), sexual maturity in these populations appears to be age-dependent, with many cod mature at 4, and all females and most males at 5 years of age. However, in Lake Charlegrark, females mature at 6 years of age and a minimum size of 2.0kg, and males at 3 - 4 years and 0.7kg (Gooley et al. 1995). In some species, slow-growing fish mature at greater ages and smaller sizes than faster growing fish (Alm 1959). The reported variation in age and size at maturity between Murray cod in NSW and Victorian waters may be due, at least partly to slower growth in the colder, southern waters.

Reproductive strategies and fisheries management

In summary, Murray cod is a large, long-lived, relatively slow-growing species which has a reproductive strategy involving a long generation period, group-synchronous oocyte development, low fecundity, a relatively complex breeding behaviour, including pairing of broodfish, spawning site selection and paternal protection of the large, adhesive eggs during a relatively short, well-defined breeding season in spring.

Such fishes have a biological advantage in that potentially high larval mortality in unfavourable breeding seasons is compensated for by repeated annual spawnings over the long life span of individuals (Giesel 1976; May 1976). However, this advantage may be lost when populations decline significantly to relatively low levels, as is the case with Murray cod (Lake 1971; Cadwallader and Backhouse 1983; Rowland 1989).

Previous research (Rowland 1983, 1985, 1989, 1992, 1998) as well as the study reported in this paper have provided base-line biological data for the formulation of fisheries management policies for Murray cod. NSW Fisheries has introduced the following restrictions for the recreational fishery for Murray cod: a 3-month closed season (September, October, November) to protect cod during the breeding season; a minimum size limit of 50cm, to ensure that most fish retained by fishers have reached sexual maturity; and a bag limit of 2 fish/day and 4 in possession to reduce fishing mortality. The size limit and closed season also apply to the inland, commercial fishery; this fishery has limits on gear (type, number, mesh size) and is restricted geographically to certain waters in south-western NSW.

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REFERENCES

Alm, G. (1959). Connection between maturity, size and age in fishes. Experiments carried out at the Kalarne fishery research station. *Institute of Freshwater Research Drottningholm Report* (40) 1–145.

Anderson, J.R., Morison, A.K. and Ray, D.J. (1992). Age and growth of Murray cod, *Maccullochella peelii* (Perciformes: Percichthyidae), in the lower Murray-Darling Basin, Australia, from thin-sectioned otoliths. *Australian Journal of Marine and Freshwater Research* **43**, 983–1013.

Bagenal, T.B. (1978). Aspects of fish fecundity. In 'Ecology of Freshwater Fish Production'. (Ed. S.D. Gerking), pp. 75–101. (Blackwell Scientific, Melbourne).

Bye, V.J. (1984). The role of environmental factors in the timing of reproductive cycles. In 'Fish Reproduction Strategies and Tactics' (Eds G.W. Potts and R.J. Wootton), pp. 187–205. (Academic Press, Sydney).

Cadwallader, P.L. and Backhouse, G.N. (1983). 'A Guide to the Freshwater Fish of Victoria'. (Government Printer, Melbourne).

Cadwallader, P.L. and Gooley, G.J. (1985). 'Propagation and Rearing of Murray Cod *Maccullochella peeli* at the Warmwater Fisheries Station Pilot Project Lake Charlegrark'. (Government Printer, Melbourne).

Dakin W.J. and Kesteven, G.L. (1938). The Murray cod (*Maccullochella macquariensis* (Cuv. et Val.)). *N.S.W. State Fisheries Research Bulletin* (1), 1–18.
de Vlaming, V. (1983). Oocyte development patterns and hormonal involvements among teleosts. In 'Control Processes in Fish Physiology' (Eds J.C. Rankin, T.J. Pitcher and R.T Duggan), pp.176–287. (Wiley Interscience, New York).
Foucher, R.P. and Beamish, R.J. (1980). Production of non-viable oocytes by Pacific Lake (*Merluccius productus*). *Canadian Journal of Fisheries and Aquatic Science* **37**, 41–48.
Giesel, J.T. (1976). Reproductive strategies as adaptations to life in temporally heterogeneous environments. *Annual Review of Ecological Systematics* **7**, 59 -79.
Gooley, G.J. (1992). Validation of the use of otoliths to determine the age and growth of Murray cod, *Maccullochella peelii* (Mitchell) (Percichthyidae), in Lake Charlegrark, Western Victoria. *Australian Journal of Marine and Freshwater Research* **43**, 1091–1102.
Gooley, G.J., Anderson, T.A. and Appleford, P. (1995). Aspects of the reproductive cycle and gonadal development of Murray cod, *Maccullochella peelii peelii* (Mitchell) (Percichthyidae), in Lake Charlegrark and adjacent farm ponds, Victoria, Australia. *Marine and Freshwater Research* **46**, 723 -728.
Gromov, I.A. (1979). The fecundity of the Eastern Carp, *Cyprinus carpio haematopterus*. *Journal of Ichthyology* **19**(1), 98–103.
Ingram, B.A. and Rimmer, M.A. (1992). Induced breeding and larval rearing of the endangered Australian freshwater fish trout cod, *Maccullochella macquariensis* (Cuvier) (Percichthyidae). *Aquaculture and Fisheries Management* **24**, 7–17.
Lake, J.S. (1967a). Rearing experiments with five species of Australian freshwater fishes. I. Inducement to spawning. *Australian Journal of Marine and Freshwater Research* **18**, 137–153.
Lake, J.S. (1967b). Rearing experiments with five species of Auatralian freshwater fishes. II. Morphogenesis and ontogeny. *Australian Journal of Marine and Freshwater Research* **18**, 155–173.
Lake, J.S. (1971). 'Freshwater Fishes and Rivers of Australia'. (Thomas Nelson, Sydney).
Lam, T.J. (1983). Environmental influences on gonadal activity in fish. In 'Fish Physiology' (Eds W.S. Hoar, D.J. Randall and E.M. Donaldson), Vol.IX, Part B, pp. 65–116. (Academic Press, Sydney).
Leggett, W.C. and Carascadden, J.E. (1978). Latitudinal variation in reproductive characteristics of American shad (*Alosa sapidissima*): evidence for population specific life history strategies in fish. *Journal of the Fisheries Research Board of Canada* **35**, 1469–1478.
Llewellyn, L.D. and MacDonald, M.C. (1980). Family Percichthyidae Australian freshwater basses and cods. In 'Freshwater Fishes of South-eastern Australia' (Ed. R.M. McDowall), pp. 142–149. (Reed, Sydney).
Mann, R.H.K., Mills, C.A. and Crisp, D.T. (1984). Geographical variation in the life-history tactics of some species of freshwater fish. In 'Fish Reproduction Strategies and Tactics' (Eds G.W. Potts and R.J. Wootton), pp. 171–186. (Academic Press, Sydney).
May, R.M. (1976). Models for single populations. In 'Theoretical Ecology Principles and Applications' (Ed. R.M. May), pp. 4–25. (W.B. Saunders Co., Philadelphia).
Mayer, I., Shackley, S.E. and Witthames, P.R. (1990). Aspects of the reproductive biology of the bass, *Dicentrarchus labraz* L. II. Fecundity and pattern of oocyte development. *Journal of Fish Biology* **36**, 141–148.
Merrick, J.R. and Schmida, G.E. (1984). 'Australian Freshwater Fishes. Biology and Management'. (J.R. Merrick, North Ryde).
Pollard, D.A., Llewellyn, L.C. and Tilzey, R.D.J. (1980). Management of freshwater fish and fisheries. In 'An Ecological Basis for Water Resource Management' (W.D. Williams), pp. 227–270. (Australian National University Press, Canberra).
Roughley, T.C. (1968). 'Fish and Fisheries of Australia'. (Halstead Press, Sydney).
Rowland, S.J. (1983). Spawning of the Australian freshwater fish Murray cod, *Maccullochella peeli* (Mitchell), in earthen ponds. *Journal of Fish Biology* **23**, 525–534.
Rowland, S.J. (1985). Aspects of the biology and artificial breeding of the Murray cod, *Maccullochella peeli*, and the eastern freshwater cod, *M. ikei* sp. nov. (Pisces: Percichthyidae). Ph.D. Thesis, Macquarie University, Sydney.
Rowland, S.J. (1988). Hormone-induced spawning of the Australian freshwater fish Murray cod, *Maccullochella peeli* (Mitchell)(Percichthyidae). *Aquaculture* **70**, 371–389.
Rowland, S.J. (1989). Aspects of the history and fishery of the Murray cod, *Maccullochella peeli* (Mitchell)(Percichthyidae). *Proceedings of the Linnean Society of New South Wales* **111**(3), 201–213.
Rowland, S.J. (1992). Diet and feeding of Murray cod (*Maccullochella peelii*) larvae. *Proceedings of the Linnean Society of New South Wales* **113**(3), 193–201.
Rowland, S.J. (1998). Age and growth of the Australian freshwater fish Murray cod, *Maccullochella peelii peelii*. *Proceedings of the Linnean Society of New South Wales*. This volume.
Stearns, S.C. and Crandall, R.E. (1984). Plasticity for age and size at sexual maturity: a life-history response to unavoidable stress. In 'Fish Reproduction Strategies and Tactics' (Eds G.W. Potts and R.J. Wootton), pp. 13–33. (Academic Press, Sydney).
Volodin, V.M. (1979). The fecundity of the perch, *Perca fluviatilus*, from Rybinsk Reservoir. *Journal of Ichthyology* **19**(4), 85–92.
Wyse, L.C. (1973). Artificial spawning of Murray cod. *Aquaculture* **2**, 429–432.